FOLIVORY AND BILL MORPHOLOGY IN THE TOOTH-BILLED BOWERBIRD, *SCENOPOEETES DENTIROSTRIS* (PASSERIFORMES: PTILONORHYNCHIDAE): FOOD FOR THOUGHT

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The Tooth-billed Bowerbird, *Scenopoeetes dentirostris*, is a facultative, arboreal, folivore. For a substantial proportion of winter diet they tear and masticate pieces of leaves, succulent buds and vine stems, but in summer they are mostly frugivorous. Specialised notches, cusps, or 'teeth' on their lower mandible cutting edges fit into reciprocal indentations in the upper mandible when the bill is closed, to more efficiently crush and masticate vegetable matter. As a result of this diet, birds commonly void compact faecal 'pellets' consisting predominantly to exclusively of finely-masticated foliage. Folivory by this passerine in the resource-rich habitat of tropical upland rainforest is surprising and may be in part due to the presence in its habitat of three closely related bowerbird, and many other frugivorous, species. Studies of Tooth-bill diet, nutrition, and associated morphology and physiology are required.
❐ *Folivory, bill morphology, bird 'teeth', mastication of foliage, Tooth-billed Bowerbird, Scenopoeetes dentirostris.*

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The Tooth-billed Bowerbird, *Scenopoeetes dentirostris* (subsequently Tooth-bill), represents a monotypic genus of the bowerbird family, Ptilonorhynchidae, whose 19 species are endemic to Australia and Papua New Guinea. It occurs only in upland rainforests between 600-1400m above mean sea level, from Mt Amos (15°42'S 145°18'E), near Cooktown, southward to Mt Elliot (19°30'S 146°57'E), just south of Townsville, N Queensland, tropical NE Australia (Nix & Switzer, 1991). Tooth-bills, like other polygynous bowerbirds, demonstrate male promiscuity and female-only nesting duties. They are, however, atypical in being sexually monomorphic, short and stout-billed, and in court-clearing males that form exploded leks (Frith & Frith, 1985a, 1993, 1994, 1995).

Male Tooth-bills clear leaf litter to form a display area on the forest floor about the base of at least one tree trunk and collect fresh large leaves to lay them paler side uppermost on this court. Courting starts with singing and court maintenance from late August to September and continues to January or early February (see Frith & Frith, 1993, 1994).

Jackson (1909, 1910), Marshall (1951, 1954) and Warham (1962) made preliminary studies of males and courts, and limited knowledge of nesting biology is summarised by Frith & Frith (1985a). Geoffrey Moore (unpubl. data) examined the role of males as plant seed dispersal agents. Court seasonality, morphology, dispersal, constancy and ownership are detailed in Frith & Frith (1994) and home range in adult males in Frith et al. (1994).

The Tooth-bill is unique among bowerbirds in having a conspicuous irregular notch or 'tooth' on the cutting edges of the upper mandible and several, more regular, cusps and notches on the tip and cutting edges of the lower mandible respectively. These 'teeth' were long considered adaptations used solely to obtain leaves for court decoration, by biting, snipping or sawing at their petioles (Marshall, 1951; Gilliard, 1969; Chaffer 1984). In support of this interpretation Marshall (1954) and Chaffer (1984) noted that the means by which Tooth-bills obtained leaves for the court was laborious and arduous; birds having to tear and saw at leaf petioles, particularly those of larger ones such as the gingers (*Alpinia* spp.). A fully-developed 'toothed' bill adorns birds of both sexes and all post-juvenile ages, while only older males (probably > 2-3 years old, pers. obs.) decorate courts with leaves.

By far the most commonly used leaves for court decoration at Paluma, near Townsville, N Queensland were those of the small tree *Polyscias australiana* (see Frith & Frith, 1994),

but this is not necessarily the case elsewhere (pers. obs.). Leaves of *P. australiana* are quickly and and easily removed from the plant by male Tooth-bills. It is possible that differing leaf attachment strengths of plants accounts for the observed differences in Tooth-bill effort in leaf removal.

Recent observations have demonstrated that Tooth-bills are partly folivorous and that the externally-toothed bill is an adaptation to this diet (Lavery & Grimes, 1974; Frith & Frith, 1979 and unpubl. data). Tooth-bills certainly use the 'tooth-like' structures of the mandible edge to cut, tear, and manipulate leaves and leaf pieces (Lavery & Grimes, 1974). However, between these external serrations lie a more sophisticated and complex set of structures, alluded to by Marshall (1954: 154) whose function equates more closely to that of 'teeth'. This contribution provides an initial description of these structures of bill and palate and illustrates graphically how they function to finely masticate foliage prior to ingestion. We do not review comprehensively the morphology, ecology, nutrition or physiology associated with this unusual passerine diet. Our aim in presenting this review of our initial findings is, as the subtitle implies, to stimulate the interest of appropriate specialists in these aspects of Tooth-bill biology.

METHODS

We studied male Tooth-billed Bowerbird sociobiology and ecology from 1978 to 1990 in rainforest near Paluma (19°00'S 146°10'E), N Queensland at an elevation of ~875m ASL. Subsequent qualitative work was carried out on the Atherton Tableland (17°25'S 145°42'E ~ 680m ASL). Intensive annual fieldwork began as soon as males started singing and/or clearing and decorating courts (September or early October at Paluma); and annual fieldwork ceased when singing and court usage declined (during January or early February). Court attendance, displays and vocalisations were monitored intensively from 7 November to 8 December 1979 and 1 October 1980 to 14 February 1981 (see Frith & Frith, 1993, 1994, 1995; Frith et al., 1994). To learn what male Tooth-bills ate during their court-attendance season we erected ~50cm^2 pieces of black nylon fine mesh ~10cm above the forest floor beneath low (<1.5m) court perches favoured by males. Excreta voided by birds from these perches accumulated on the nylon and were collected weekly for subsequent analysis (Frith & Frith, 1994 & unpubl. data). As males spent on average 64% of daylight upon such favoured perches during their peak display season (Frith & Frith, 1994, 1995) faecal samples were large. Because Tooth-bills swallow whole the vast majority of fruits they eat (larger figs, *Ficus* spp, excepted) seeds are intact, and no regurgitation occurs, these samples represent an accurate indication of fruit diet. In addition to work on males at courts, the feeding ecology of the species was examined by recording all observed bowerbird foraging during 1,360hrs of standardised transect and quadrat observation and an additional 187h of random observation through Tooth-bill habitat. These observations resulted in 533 records of Tooth-bills feeding upon plants.

Subsequent to the report that Tooth-bills eat foliage by tearing leaves, buds and vine stems and manipulating and masticating them prior to ingestion (Lavery & Grimes, 1974; Frith & Frith 1979), we closely examined the bill of several living and preserved Tooth-bills for physical adaptations to such folivory.

RESULTS

Tooth-bill folivory typically involved a quietly perched solitary bird biting or tearing off pieces of fresh leaf or vine stem growth. Once a larger piece of leaf was removed from the plant it was rapidly, skillfully and repeatedly 'folded' in the mandible tips into a compact wad. This was then masticated or 'chewed' between the mandible tips before being ingested; green fluid resulting from the mastication often visibly accumulated at the tip of the mandibles (Frith & Frith, 1979) and presumably with some ingested.

The majority of Tooth-bill excreta accumulated beneath favoured court perches consisted of an amorphous mass (with some, more recently produced, discrete faecal 'pellets') of fruit pericarp and seeds, the quantity of this increasing during seasonal peak court attendance (Frith & Frith, 1995). Some 5 to 10% of monthly excreta samples consisted of faecal 'pellets' predominantly or exclusively composed of finely-masticated vegetable matter (see Figs 1 & 2A). The smaller samples of such faecal matter for Oct-Dec, compared with Sept, 1979 are due to lower court attendance levels by males due to unseasonally dry conditions (Frith & Frith, 1994). It must be noted that the percentages in Fig. 1 for leaf matter are minimal because we scored each entire pellet of same as one 'leaf' record whereas the remaining mass of fruit

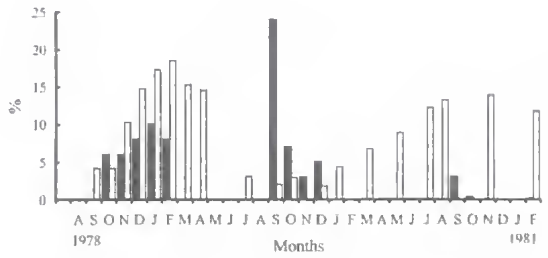

FIG. 1. Pereentage of total weekly exereta samples, eolleeted beneath eourt perches favoured by eourt-attending male Tooth-billed Bowerbirds, eonsisting of faeeal pellets primarily of mastieated leaf matter (solid bars) and the pereentage of sampled trees that were bearing fruit (open bars) over three eourtship seasons (see text).

remains were scored by constituent fruits (as indicated by seed numbers). While these data were only obtainable during the months that males attended courts they do suggest an increase in folivory when fewer fruits were available in the habitat (see Fig. 1, text below, and Frith & Frith, 1995, 1998).

While details of direct observations of Tooth-bill foraging will be presented elsewhere, we note that of 533 records of feeding upon plant material observed, 79% were upon fruits and 21% (n = 111) upon other plant material as follows: leaves (n = 90), flowers (8), succulent stems (7) and buds (6). We stress that we consider this 21% of annual diet as folivory to be a gross underestimate, because Tooth-bills eating foliage (particularly during winter when they become silent, secretive and inactive in the forest canopy) are extremely cryptic while birds taking fruit are much more conspicuous because fruiting plants attract numerous bowerbirds and other frugivorous birds (pers. obs.).

During winter, Tooth-bills become so elusive that some observers believed they left their upland rainforest breeding habitat (e.g. Green, 1910). As a percentage of directly-observed Tooth-bill foraging events, folivory increased during periods of least fruit availability within the habitat (Fig. 1). The percentage of directly observed folivory was >20% but at times may reach 25-40% (Fig. 3) which, for winter months at least, we consider an underestimate (as above). The gizzard of a male Tooth-bill that died on 14 June 1989 contained 7.8g of finely-masticated leaf mash (see Fig. 2b); the entire gut being full of finely-textured green leafy slime.

DISCUSSION

FOLIVORY. Habitual folivory is a rare trait among birds. However, the New Zealand avifauna is exceptional in this regard, having evolved in the absence of competion from browsing mammals (I. Flux, pers. comm.). A notable terrestrial and arboreal folivore is the flightless, nocturnal, Kakapo, *Strigops habroptilus*, an extraordinary parrot endemic to New Zealand temperate forests which browses plants by masticating leaves and fronds, often in situ on some plants (Merton, 1985). Elsewhere folivory is common typically among the non-passerine groups of: waterfowl, which feed upon aquatic vegetation or graze upon terrestrial grasses and herbage; some terrestrial game bird groups including the palearctic Black Grouse, *Tetrao tetrix*, and Western Capercaillie, *Tetrao urogallus* (Phasianidae), (Dorst, 1974); some rails; and several other species (Dorst, 1974: 70; Morton, 1978; Carboneras, 1992; Taylor, 1996). True folivory is also well known in the extraordinary, neotropical, Hoatzin (*Opisthocomus hoazin*, an aberrant cuckoo) that lives in riverine gallery forest subject to flooding (Dominguez-Bello et al., 1994; Thomas, 1996)

Folivory is particularly rare among arboreal passerines. It is known, however, as typical foraging in the three neotropical plantcutters (*Phytotoma* spp., Cotingidae: Küchler, 1936; Ames, 1971; Lanyon & Lanyon, 1989; Sibley & Ahlquist, 1990) of open woodland and scrub (Ridgely & Tudor, 1994) and in three species of saltator (*Saltator* spp., Emberizidae) of secondary growth, gardens, plantations and forest edge (Jenkins, 1969; Stiles & Skutch, 1989). The Kokako (*Callaeas cinerea*, Callaeidae) of New Zealand temperate forests is conspicuously folivorous and will eat yellowing, dehiscent, or even brown and dead, leaves of some plants (Hay, 1985; I. Flux, pers. comm.; pers. obs.). It is also known in the Common Bullfinch, *Pyrrhula pyrrhula* (Fringillidae), and several other species (Dorst, 1974) which eat buds more than leaves, but is otherwise only occasionally observed as an irregular and small dietary component in few passerine species (i.e. some birds of paradise and bowerbirds: Frith & Frith, 1979; Donaghey, 1981, 1996; Frith & Beehler, 1998). It is doubtless more widespread than is indicated by present knowledge.

It has been noted that Hoatzin selectively eat 'young leaves, tender shoots and buds, which are higher in water content, as well as being both

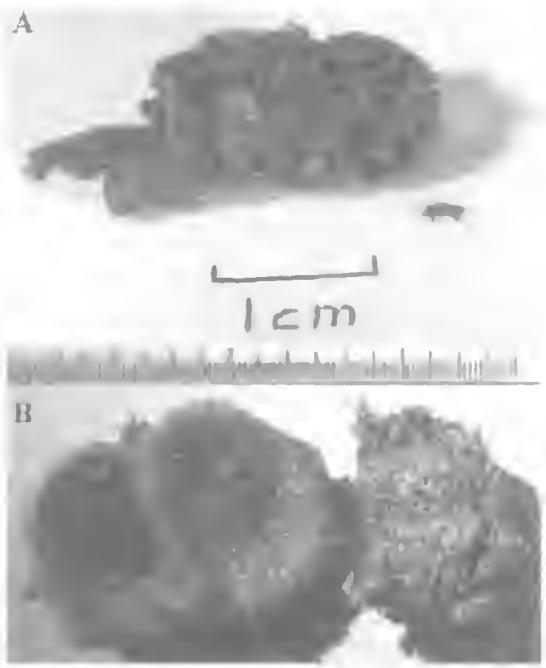

FIG. 2. A, fresh Tooth-billed Bowerbird faecal pellet consisting predominantly of finely-masticated leaf matter with 1cm scale indicated. B, freshly dissected Tooth-billed Bowerbird gizzard (left) and its content (right) of finely-masticated leaf matter (ruler with 1 and 5mm markings). Both near Paluma, Queensland, June 1989.

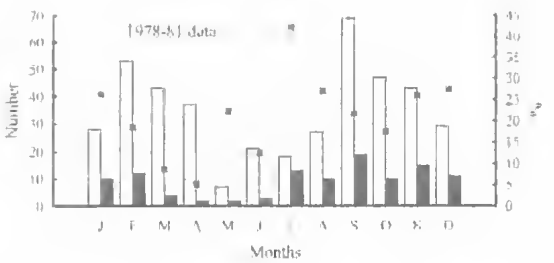

FIG. 3. Number (left axis) of observations of Tooth-billed Bowerbird feedings near Paluma, Queensland, upon fruit (open bars) and foliage (solid bars), and the percentage (right axis) records of foliage eating represented of total feeding events during each month (line curve with solid squares). Data for August 1978-February 1981 inclusive are combined.

easier to digest and more nutritious' (Thomas, 1996). This statement applies equally to the Tooth-bill in our experience. The Hoatzin is remarkable, however, in that its crop and lower oesophagus are its main digestive organs. Hoatzins ferment vegetation in the foregut in a similar way to the gut fermentation of cattle (Strahl et al., 1989; Dominguez-Bello et al., 1993; Thomas, 1996). Physiological adaptations to the digestion of such an unusual and presumably low carbohydrate/energy diet, such as an (if only seasonally) elongated gut (see Sibly, 1981), might be expected. These have not, however, been looked for in Tooth-bills, or in the several other bowerbird species which also eat foliage to a lesser extent. We did not investigate the relative nutritional values of plant foliage eaten by Tooth-bills, and this remains a field for future study.

Foliage represents a dietary component low in readily available carbohydrate/energy content (Sun et al., 1997; Powlesland et al., 1997). The energetic disadvantage of small body size probably limits folivory in passerines, this diet being far more common in larger birds and especially those with fewer predators. That this rare avian diet and associated bill adaptations occur in the Tooth-bill begs the obvious question: why so in this passerine? It is possible that lower fruit resource availability in winter has resulted in the need for obligate frugivores to perform folivory as an adaptation to winter survival, but supporting data are few (Figs 1 & 3; Frith & Frith, 1998, fig. 2c). An adequate answer will doubtless require considerable research and time. It has been noted that the extraction of energy from leaves requires a relatively long food retention time and that large quantities must be ingested and stored; circumstances which present major disadvantages for flying animals (Morse, 1975; Morton, 1978; Sibly, 1981). An alternative strategy is for rapid throughput of plant material with minimal digestion (Sibly, 1981). The Tooth-bill remains markedly inactive and apparently flies little during the winter months, when folivory quite possibly dominates its diet. Thus the low energetic demands of eating (abundant) leaves might outweigh the costs of seeking (sparse) winter fruits. As predator pressure may be important in explaining why folivory is rare in birds (Morton, 1978), particularly in passerines, the highly cryptic plumage and folivorous foraging of both sexes of the Tooth-bill are noteworthy.

Satin Bowerbirds, *Ptilonorhynchus violaceus*, form flocks in the winter to early spring and then, typically, eat terrestrial herbs and grasses in both rainforest and woodland (Donaghey, 1981; Vellenga & Vellenga, 1985; pers. obs.). These plants may represent a seasonally significant proportion of their diet (c. 50-80% according to

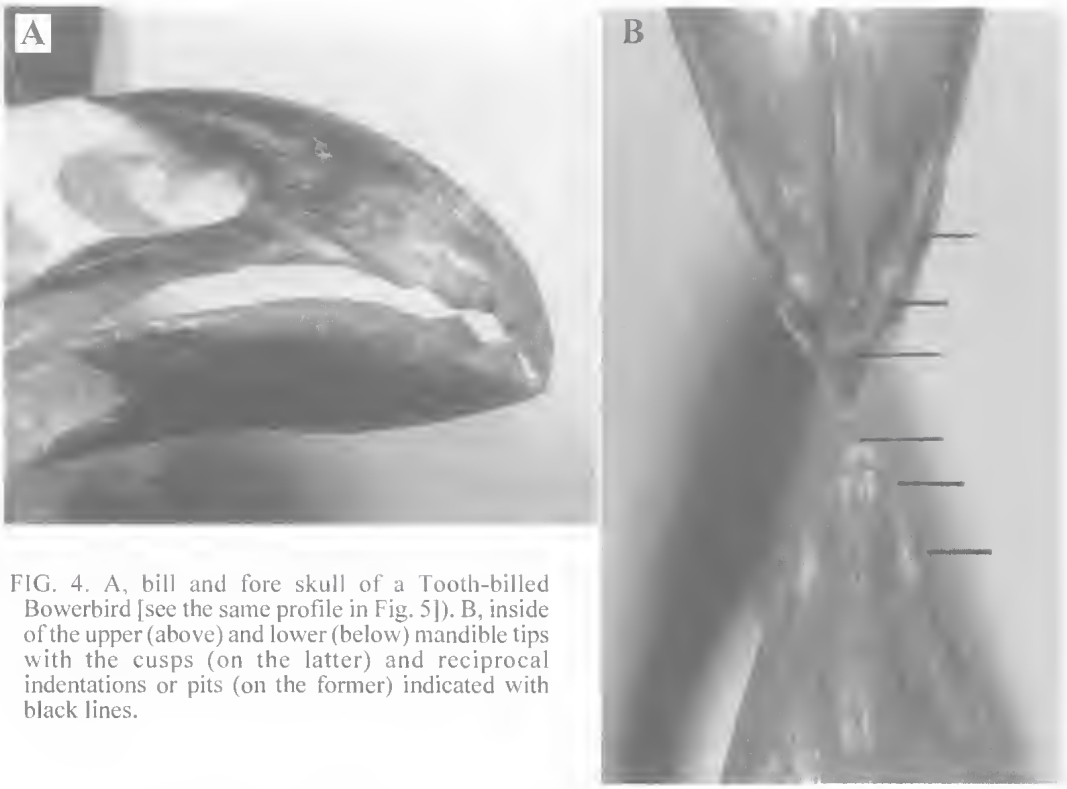

FIG. 4. A, bill and fore skull of a Tooth-billed Bowerbird [see the same profile in Fig. 5]). B, inside of the upper (above) and lower (below) mandible tips with the cusps (on the latter) and reciprocal indentations or pits (on the former) indicated with black lines.

Donaghey, 1981). Satin Bowerbirds appear to 'chew' leaf matter in the mandible tips prior to ingesting it. Male Satin Bowerbirds (and other avenue bower building species) also masticate foliage to produce 'paint' which they apply to the inner surface of bower walls (Marshall, 1954; Gilliard, 1969; Donaghey, 1996; pers. obs.). It should be noted, however, that Satin Bowerbirds, including those populations (*P. v. minor*) sympatric with Tooth-bills do so in habitats adjacent to, but outside, the rainforsts within which Tooth-bills perform their winter folivory (Frith & Frith, unpubl. data).

Donaghey (1981, 1996) found that Satin Bowerbirds living in subtropical woodland ate more leaves during winter to early spring, than those living in adjacent rainforest, suggesting that the latter area was richer in other foods. As tropical rainforests are rich in diverse avian food resources it is surprising to find substantial folivory in the Tooth-bill. The Tooth-bill is sympatric with three, predominantly frugivorous bowerbirds (Spotted Catbird, *Ailuroedus melanotis*, Satin Bowerbird and Golden Bowerbird, *Prionodura newtoniana*) and a number of other, obligate, frugivores. This may have played some role in the evolution of its folivory through interspecific competition (Lack, 1971; Lavery & Grimes, 1974), particularly during strong competitive pressure exerted by lean seasons. In the upland wet tropical rainforest habitat of the Tooth-bill, the winter months are resource-poor with respect to both arthropods (Frith & Frith, 1985b; Frith, D. & Frith, C., 1990), which female Tooth-bills feed to their offspring as a small proportion of their diet, and fruits (Frith & Frith, 1994). Such a scenario might, in addition to a lack of predators, have in part influenced the evolution of partial folivory in the New Zealand Kokako as this (now endangered) passerine shared much of its habitat with two, predominatly insectivorous, closely related members of the same family (the Saddleback, *Philesturnus carunculatus* and the, now extinct, Huia, *Heteralocha acutitostris*). The folivorous, and now endangered, flightless Kakapo similarly shared habitat with up to four other New Zealand endemic parrot species.

BILL MORPHOLOGY. With respect to fruits, Tooth-bills are 'gulpers' (Levey, 1990) in that they swallow fruits whole with their seed(s) intact, do not typically use their 'teeth' to remove

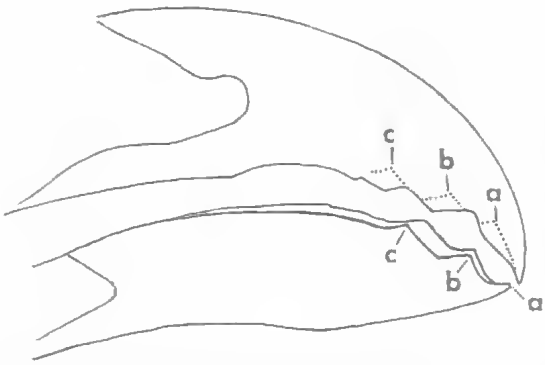

FIG. 5. A simplified schematic diagram of a Tooth-billed Bowerbird bill in profile showing how the cusp at the tip of the lower mandible (lower a) and those on its cutting edges (lower b & c) fit into the reciprocal indentations (dotted lines) in the upper mandible (upper a,b &c) when the mandibles are closed to masticate foliage. See also Fig. 4.

flesh of large-seeded fruits, and do not regurgiate seeds. The more easily digested nutrients, of proteins and soluble carbohydrates, in plant foliage cells are protected by cellulose walls which vertebrates lack the enzymes to digest, and the cell walls must therefore be mechanically broken up (Sibly, 1981). Details of direct observation of feeding Tooth-bills combined with knowledge gained by examination of several preserved and living individuals suggest to us that: a) the cutting edges of the reciprocal mandibular notches (Fig. 4a) are used to bite or tear and then manipulate and fold leaf pieces into a compact wad prior to mastication, and that b) the lower mandible 'teeth', used in a 'chewing' action, enhance digestibility of foliage by crushing and grinding. Thus the 'teeth' serve to break up the cell walls of the foliage. The nature of voided faecal 'pellets' of masticated leaf matter (Fig. 2a) suggest that Tooth-bills might not digest plant fibre, as does the Hoatzin, but merely break down plant cells and so release their digestable content; but this requires experimental study. Certainly male Tooth-bills at their courts do not regurgitate indigestable fibre as do many frugivores.

The most important point concerning the Tooth-bill's use of lower mandibular 'teeth' is that their five functional tips, or cusps, fit perfectly into reciprocal indentations, or pits, in the under surface of the distal premaxilla (see Figs 4, 5). These specialised structures form efficient grinding 'teeth' for Tooth-bills by creating pressure points for foliage mastication (Fig. 6). Notwithstanding their folivory, there is no comparable sophistication of bill morphology in Satin Bowerbirds.

Various bill modifications to deal with vegetable matter are known in the waterfowl (Johnsgard, 1968) and some other groups (see above). We were able to briefly examine a freshly-thawed Kokako specimen while in New Zealand in May 1998 and found structures on the central palate of the upper premaxilla that may function in mastication of vegetable matter. However, this possibly novel adaptation awaits confirmation in additional specimens, and an understanding of its function, and formal description (I. Flux, pers. comm.).

It is noteworthy that the considerable literature on the Hoatzin and its folivorous diet does not appear to allude to any kind of mastication of vegetation or to morphological adaptations of the inner mandibles for doing so (Thomas, 1996 & references therein). However, the cutting edges

FIG. 6. Part of the base of a *Polyscias australiana* leaf found freshly laid upon a Tooth-billed Bowerbird court as a court decoration. Note that the 'bruise' marks left by the bird's bill clearly indicate the pressure points where the five lower mandible cusps meet the reciprocal indentations (indicated) in the upper mandible (see Figs 4, 5).

of the mandibles of the three neotropical plant-cutters are conspicuoulsy serrated, presumably to enhance their cutting (and masticating?) function. While many of the pan-tropical (Australasia excluded) non-passerine barbets (Piciformes, Capitonidae) show a diversity of conspicuously notched or 'toothed' mandible edges, no evidence to suggest these might be used in folivorous feeding appears to exist notwithstanding long-term intensive collecting and observation of African and Asian species. A recent review of diets of all African species makes no mention of foliage found in birds or seen to be eaten by them (Short & Horne, 1988). The Great Barbet, *Megalaima virens*, has a long but visibly unnotched or 'toothed' bill but has, however, been noted to avidly eat flower petals by 'the whole flower being first revolved and crushed in the mandibles and compacted into boluses of crumpled petals' (Ali & Ripley, 1970). The same authors note that the Green Barbet, *M. zeylanica*, eats flower petals.

We suggest that the mandibles and palate of specimens of all folivorous birds, and any suspected of being so, be examined for the possible presence of structures for the mastication of foliage as this might prove instructive. There can be no doubt that studies of Tooth-bill diet, nutrition, and associated morphology and physiology will prove rewarding in the broad context of avian folivory.

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LITERATURE CITED

ALI, S. & RIPLEY, S.D. 1970. Handbook of the birds of India and Pakistan. Volume 4. (Oxford University Press: Bombay).

AMES, P.L. 1971. The morphology of the syrinx in passerine birds. Bulletin of the Peabody Museum of Natural History 37: 1-194.

CARBONERAS, C. 1992. Family Anatidae. In del Hoya, J., Elliot, A. & Sargatal, J. (eds) Handbook of the birds of the world. Vol. 1. (Lynx Edicions: Barcelona).

CHAFFER, N. 1984. In quest of bowerbirds. (Rigby: Adelaide).

DOMINGUEZ-BELLO, M.G., LOVERA, M., SUÁREZ, P. & MICHELANGELI, F. 1993. Microbial inhabitants in the crop of the Hoatzin (*Opisthocomus hoazin*): The only foregut fermenter avian. Physiological Zoology 66: 374-383.

DOMINGUEZ-BELLO, M.G., MICHELANGELI, F., RUIZ, M.C., GARGIA, A. & RODRIGUEZ, E. 1994. Ecology of the folivorous Hoatzin (*Opisthocomus hoazin*) on the Venezualan plains. Auk 111: 643-651.

DONAGHEY, R.H. 1981. The ecology and evolution of bowerbird mating systems. Unpublished PhD Thesis, Department of Zoology, Monash University, Melbourne.

1996. Bowerbirds. In Strahan, R. (ed.) Finches, bowerbirds & other passerines of Australia. (Angus & Roberstson: Sydney).

DORST, J. 1974. The life of birds. Vol. 1. (Weidenfeld & Nicolson: London).

FRITH, C.B. & BEEHLER, B.M. 1998. The birds of paradise: Paradisaeidae. (Oxford University Press: Oxford).

FRITH, C.B. & FRITH, D.W. 1979. Leaf eating by birds of paradise and bowerbirds. Sunbird 10: 21-23.

1985a. Parental care and investment in the Tooth-billed Bowerbird, Scenopoeetes dentirostris (Ptilonorhynchidae). Australian Bird Watcher 11: 103-113.

1985b. Seasonality of insect abundance in an Australian upland tropical rainforest. Australian Journal of Ecology 10: 237-248.

1993. Courtship display of the Tooth-billed Bowerbird *Scenopoeetes dentirostris*; its behavioural and systematic significance. Emu 93: 129-136.

1994. Courts and seasonal activities at them by male Tooth-billed Bowerbirds *Scenopoeetes dentirostris* (Ptilonorhynchidae). Memoirs of the Queensland Museum 37: 121-145.

1995. Court site constancy, dispersion, male survival and court ownership in the male Tooth-billed Bowerbird, *Scenopoeetes dentirostris* (Ptilonorhynchidae). Emu 95: 84-98.

1998. Nesting biology of the Golden Bowerbird *Prionodura newtoniana* endemic to Australian upland tropical rainforest. Emu 98: 245-268.

FRITH, D.W. & FRITH, C.B. 1990. Seasonality of litter invertebrate populations in an Australian upland tropical rain forest. Biotropica 22: 181-190.

FRITH, C.B., FRITH, D.W. & MOORE, G.J. 1994. Home range and extra-court activity in the male Tooth-billed Bowerbird *Scenopoeetes dentirostris* (Ptilonorhynchidae). Memoirs of the Queensland Museum 37: 147-154.

GILLIARD, E.T. 1969. Birds of paradise and bower birds. (Weidenfeld & Nicolson: London).

GREEN, B. 1910. Tooth-billed Bower-bird. Emu 9: 247.

HAY, J.R. 1985. Kokako *Callaeas cinerea*. In Robertson, C.J.R (ed.) Reader's Digest complete book of New Zealand birds. (Reader's Digest: Sydney).

JACKSON, S.W. 1909. In the Barron River Valley, North Queensland. Emu 8: 233-285.

1910. Additional notes on the Tooth-billed Bower-bird (*Scenopoeetes dentirostris*) of North Queensland. Emu 10: 81-88.

JENKINS, R. 1969. Ecology of three species of Saltators, with special reference to their frugivorous diet. PhD thesis, Harvard University.

JOHNSGARD, P.A. 1968. Waterfowl – their biology and natural history. (University of Nebraska Press: Lincoln).

KÜCHLER, W. 1936. Anatomische untersuchungen an *Phytotoma rara* Mol. Journal für Ornithologie 84: 352-362.

LACK, D. 1971. Ecological isolation in birds. (Blackwell Scientific Publications: Oxford).

LANYON, S.M. & LANYON, W.E. 1989. The systematic position of the plantcutters, *Phytotoma*. Auk 106: 422-432.

LAVERY, H.J. & GRIMES, R.J. 1974. The functions of the bill of the Tooth-billed Bowerbird. Emu 74: 255-256.

LEVEY, D.J. 1990. Digestive processing of fruits and its consequences for fruit-frugivore coevolution. Acta XX Congressus Internationalis Ornithologici: 1624-1629.

MARSHALL, A.J. 1951. Leaf-display and the sexual cycle in the Tooth-billed 'Bowerbird' (*Scenopoeetes dentirostris*, Ramsay). Proceedings of the Zoological Society of London 120: 749-758.

1954. Bower Birds – their displays and breeding cycles. (Oxford University Press: Oxford).

MERTON, D.V. 1985. Kakapo *Strigops habroptilus*. In Robertson, C.J.R. (ed.) Reader's Digest complete book of New Zealand birds. (Reader's Digest: Sydney).

MORSE, D.H. 1975. Ecological aspects of adaptive radiation in birds. Biological Review 50: 167-214.

MORTON, E.S. 1978. Avian arboreal folivores: Why not? In Monomery, G.G. (ed.) The ecology of arboreal folivores. (Smithsonian Institution Press: Washington, DC).

NIX, H.A. & SWITZER, M.A. 1991. Rainforest animals – atlas of vertebrates endemic to Australia's Wet Tropics. Kowari 1: 1-112.

POWLESLAND, R.G., DILKS, P.J., FLUX, I.A., GRANT, A.D. & TISDALL, C.J. 1997. Impact of food abundance, diet and food quality on the breeding of the fruit pigeon, Parea *Hemiphaga novaeseelandiae chathamensis*, on Chatham Island, New Zealand. Ibis 139: 353-365.

RIDGELY, R.S. & TUDOR, G. 1994. The birds of South America. Vol. 2. (Oxford University Press: Oxford).

SHORT, L.L. & HORNE, J.F.M. 1988. The Birds of Africa. Vol. 3. (Academic Press: London).

SIBLEY, C.G. & AHLQUIST, J.E. 1990. Phylogeny and classification of birds. (Yale University Press: New Haven).

SIBLY, R.M. 1981. Strategies of digestion and defecation. In Townsend, C.R. & Calow, P. (eds) Physiological ecology – an evolutionary approach to resource use. (Blackwell Scientific Publications: Oxford).

STILES, F.G. & SKUTCH, A.F. 1989. A Guide to the birds of Costa Rica. (Helm: London).

STRAHL, S.D., PARRA, R., DOMINGUEZ, M.G. & NEHER, A. 1989. Foregut fermentation system in the Hoatzin, a neotropical leaf-eater bird. Science 245: 1236-1238.

SUN, C., MOERMOND, T.C. & GIVNISH, T.J. 1997. Nutritional determinants of diet in three turacos in a tropical montane forest. Auk 114: 200-211.

TAYLOR, P.B. 1996. Family Rallidae. In del Hoya, J., Elliot, A. & Sargatal, J. (eds) Handbook of the birds of the World. Vol. 3. (Lynx Edicions: Barcelona).

THOMAS, B.T. 1996. Order Opisthocomiformes. In del Hoya, J., Elliot, A. & Sargatal, J. (eds) Handbook of the birds of the World. Vol. 3. (Lynx Edicions: Barcelona).

VELLENGA, S. & VELLENGA, R. 1985. Notes on the food cycle of the Satin Bowerbird *Ptilonorhynchus violaceus*. The Bird Observer 643: 74-75.

WARHAM, J. 1962. Field notes on Australian bower-birds and cat-birds. Emu 62: 1-30.